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Published in:
Hearing Research

DOI:
10.1016/j.heares.2019.107835

Publication date:
2020

Hearing Research 385 (2020) 107835

Contents lists available at ScienceDirect

Hearing Research

journal homepage: www.elsevier.com/locate/heares

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ARTICLE INFO

Article history:
Received 9 May 2019
Received in revised form
30 September 2019
Accepted 27 October 2019
Available online 1 November 2019

Keywords:
Auditory
Frequency selectivity
Spontaneous otoacoustic emission
Suppression
Barn owl

ABSTRACT

Spontaneous otoacoustic emissions (SOAEs) have been observed in a variety of different vertebrates, including humans and barn owls (*Tyto alba*). The underlying mechanisms producing the SOAEs and the meaning of their characteristics regarding the frequency selectivity of an individual and species are, however, still under debate. In the present study, we measured SOAE spectra in lightly anesthetized barn owls and suppressed their amplitudes by presenting pure tones at different frequencies and sound levels. Suppression effects were quantified by deriving suppression tuning curves (STCs) with a criterion of 2 dB suppression. SOAEs were found in 100% of ears (n = 14), with an average of 12.7 SOAEs per ear. Across the whole SOAE frequency range of 3.4–10.2 kHz, the distances between neighboring SOAEs were relatively uniform, with a median distance of 430 Hz. The majority (87.6%) of SOAEs were recorded at frequencies that fall within the barn owl's auditory fovea (5–10 kHz). The STCs were V-shaped and sharply tuned, similar to STCs from humans and other species. Between 5 and 10 kHz, the median Q_{10dB} value of STC was 4.87 and was thus lower than that of owl single-unit neural data. There was no evidence for secondary STC side lobes, as seen in humans. The best thresholds of the STCs varied from 7.0 to 57.5 dB SPL and correlated with SOAE level, such that smaller SOAEs tended to require a higher sound level to be suppressed. While similar, the frequency-threshold curves of auditory-nerve fibers and STCs of SOAEs differ in some respects in their tuning characteristics indicating that SOAE suppression tuning in the barn owl may not directly reflect neural tuning in primary auditory nerve fibers.

1. Introduction

Spontaneous otoacoustic emissions (SOAEs) are sounds that are emitted by the inner ear in the absence of any stimulation. They can be recorded using a sensitive microphone in the ear canal. SOAEs appear as amplitude-stabilized signals and evidence suggests that they reflect properties of hair cells (Brownell, 1990; Manley, 2000; Kemp, 2002). Only about 60–70 percent of young, normal-hearing humans have recordable SOAEs (Talmadge et al., 1993), an indication that SOAEs are not essential for sensitive hearing in humans. Similarly, SOAEs are not shown by most laboratory animals, although their hearing sensitivity is normal. It is not yet clear why most mammalian species that were studied do not have detectable SOAEs.

Despite great variation of the inner ear anatomy, SOAEs have been described from all land vertebrate classes (e.g.: mammals: Kemp, 1979; Ohyama et al., 1991; Talmadge et al., 1993, birds: Manley and Taschenberger, 1993; Taschenberger and Manley, 1997, lizards: Köppl and Manley, 1993; Manley, 2000, 2001, 2004, and amphibians: Palmer and Wilson, 1982; van Dijk and Manley, 2001). SOAEs share characteristics across species (Köppl, 1995; Bergevin et al., 2015), suggesting that they represent a fundamental inner ear characteristic (Bergevin et al., 2015; Manley, 2000, 2001). In lizard species, the characteristic and selective effects of suppressive

Abbreviations: SOAE, Spontaneous otoacoustic emission; SPL, Sound pressure level re: 20 μPa; STC, Suppression tuning curve; TC, tuning curve; $f_{average}$, average f_{SOAE} from two recordings; f_{SOAE}, SOAE frequency; f_{tip}, STC tip frequency; CF, Characteristic frequency

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https://doi.org/10.1016/j.heares.2019.107835

tones, which enable building suppression tuning curves (STCs), show remarkable resemblances to the excitatory threshold tuning curves of single, auditory-nerve fibers (Manley and Köppl, 2008). Even though otoacoustic emissions were initially described 40 years ago (Kemp, 1979), details regarding their origin and their significance for inner-ear function remain unexplained.

The fact that avian hair cells are able to regenerate and maintain their functionality (Langemann et al., 1999; Smolders, 1999; Ryals et al., 2013; Krumm et al., 2017) has placed birds in the focus of hearing research. Previous behavioural studies showed that starlings, *Sturnus vulgaris,* and barn owls, *Tyto alba*, do not develop presbycusis during their lifetime (Langemann et al., 1999; Krumm et al., 2017). Moreover, the avian basilar papilla is homologous to the mammalian cochlea (Manley and Köppl, 1998; Köppl, 2011; Manley, 2000, 2017) and the hearing range of barn owls covers frequencies from below 500 Hz to above 10 kHz and is thus very similar to the human range of acoustic perception (Konishi, 1973). Behavioral tests also showed that birds and mammals perform similarly when discriminating frequency or level (Dooling, 1982; review: Köppl, 2015).

Avian hearing organs have two types of hair cells that grade into each other. Of these, the short hair cells, that are defined by their lack of an afferent innervation (Fischer, 1992; Manley and Gleich, 1992; Köppl, 2011), show functional similarities to mammalian outer hair cells (Beurg et al., 2013) and may be involved in active amplification (Manley and van Dijk, 2008). Despite characteristic differences in the details of their ear morphologies, SOAE suppression has been demonstrated in both birds and mammals and thus allows the intra- and interspecific evaluation and comparison of frequency tuning. Understanding the SOAE properties of barn owls might help elucidate their source and contribute to our general understanding of frequency selectivity.

The barn owl represents a highly specialized species and is established as a model organism for hearing research. By relying on acoustic cues, this animal can localize and catch its prey with high precision even in complete darkness (Payne, 1971; Konishi, 1973). Compared to other bird species, barn owls perceive higher frequency sounds (Konishi, 1973; Dyson et al., 1998; Krumm et al., 2017) and, due to the effects of the facial ruff, at lower sound pressure levels (review: Köppl, 2015). Moreover, the inner ear of the barn owl is complex and large, being 12 mm long (Fischer et al., 1988). In most birds, such as pigeons (Smolders et al., 1995) or chickens (Fischer, 1992), the basilar papillae are only approximately 5 mm long. The auditory sensitivity range of the barn owl ear covers about 5 octaves. Extraordinarily, the barn owl cochlea has an auditory fovea in which the highest-frequency octave (above 5 kHz) occupies half of the entire papilla (Köppl et al., 1993). Barn owls also perform remarkably fast temporal processing, with neuronal phase locking up to 10 kHz, i.e. more than an octave above the frequency ranges of phase locking shown in any other species (Köppl, 1997b).

To date, the barn owl is the only bird species in which SOAEs have been detected. Comparisons between mammalian and non-mammalian SOAEs reveal profound similarities, even though the anatomical properties of the inner ears differ significantly (Manley, 2001; Bergevin et al., 2008, 2015). Although a previous study demonstrated the existence and basic properties of SOAEs in barn owls (Taschenberger and Manley, 1997), the sample was limited due to the relatively poor sensitivity of the recording systems at that time.

Suppression of SOAEs by external tonal stimuli has been explored in several species and provides a non-invasive measure of inner-ear frequency selectivity (barn owl: Taschenberger and Manley, 1997, bobtail lizard: Köppl and Manley, 1994, Macaque: Martin et al., 1988, human: Zizz and Glattke, 1988; Manley and van Dijk, 2016). Moreover, it provides insight into inner ear mechanics, and in humans has been suggested to probe standing waves in the inner ear (Manley and van Dijk, 2016; Epp et al., 2018). In this respect it is not important whether the loss of amplitude in the presence of added tones is due to true suppression or to entrainment by the external tone. In this report, we use the term “suppression tuning”.

Using a more sensitive and partly automated data acquisition system in this study as compared to the previous report (Taschenberger and Manley, 1997), we obtained a larger SOAE sample and compare details of STCs of barn owls to neuronal tuning curves from nerve fiber recordings in the same species (Köppl, 1997a, b, and unpublished results).

2. Material and methods

2.1. Animals

The measurements were carried out on seven adult barn owls (*Tyto alba*), aged between 1.5 and nearly 5 years, from the breeding colony of the Carl von Ossietzky University Oldenburg, Germany. The protocol was approved by the relevant government agency (LAVES, Oldenburg, Germany; permit number 33.9-42502-04-13/1182). Animals were lightly anesthetized with a combination of ketamine and xylazine to prevent movement during the measurements. They were deprived of food 12 h previously and the initial intramuscular (i.m.) injections were given immediately after capture, to minimize stress levels during the entire procedure. Initial doses were 3 mg/kg xylazine (2%, Medistar, Serumwerk Bernburg AG), and 10 mg/kg ketamine (10%, Bela-pharm GmbH & Co. KG). Light anesthesia was maintained with i.m. injections of maximally half of the initial doses every 30–100 min. The owls were placed in a double-walled, sound-attenuating chamber (Industrial Acoustics Company, Niederkrüchten, Germany) during the entire measurement. To maintain the animal’s temperature between 39 and 40 °C, the body was wrapped in a feedback-controlled heating blanket connected to a rectal thermometer (Harvard Apparatus, Holliston, Massachusetts, USA). Other vital parameters, such as breathing and the electrocardiogram, were recorded via needle electrodes in muscles of a wing and the contralateral leg, and monitored using an oscilloscope and auditory monitor outside the chamber. The animals breathed unaided. The beak was fixed in a custom-made holder that maintained the position of the head during the measurements. Since middle-ear pressure in birds may fall to unnatural values under anesthesia (review: Larsen et al., 2016), the middle ear was vented via a 19G hypodermic needle set in the middle ear cavity on one side. This vent was maintained through the entire experiment. At the conclusion of the measurements, the cannula was removed and the skin incision sutured. The owl then received an i.m. injection of 0.02 ml meloxicam (2 mg/ml, “Metacam”, Boehringer, Ingelheim) as an analgesic and anti-inflammatory agent for the recovery phase.

2.2. Recording procedure

Both ears of each owl were examined for the presence of SOAEs. The recording procedure encompassed three main steps: 1: A recording of the sound field in the ear canal without external stimuli (2-min of recording for five ears; 5-min in nine ears). 2: The suppression measurement, during which the SOAE signal was recorded while tones over a large number of levels and frequencies were presented in quasi-random sequence. The duration of this measurement was approximately 35 min and depended on the number of stimuli presented. 3: A further SOAE recording in quiet of 2 min (equivalent to step 1), to record reference values for the SOAEs and evaluate possible shifts.

2.3. SOAE recording

An Etymotic ER10-C microphone-speaker system (Etymotic Research, Inc., Elk Grove Village, IL, USA) with a soft foam ear plug was placed at the entrance to the external ear canal, thus occluding it. The output of the microphone was amplified by 20 dB using an Etymotic ER-10C DPOAE probe driver-preamplifier (except for one individual, where a 40 dB amplification was used). To monitor the SOAE, the amplified signal was fed into a spectrum analyzer (Stanford Research System, model SR 760), covering a frequency range from 0 kHz to 16 kHz. An Audiofire ESI U 24 XL AD/DA converter (ESI Audiotechnik GmbH, Leonberg, Germany) was used to record the microphone signal on a computer disk and to generate stimuli. This converter was controlled by custom routines developed with Matlab software (2016a, MathWorks Inc., Natick, MA, USA). The AD and DA conversion were performed at 24-bit resolution and a 48 kHz sampling rate.

SOAEs were identified as peaks exceeding the noise floor and that in the averaged spectrum were suppressible by external tones. Moreover, SOAEs were individual for each ear and identifiable in both baseline measurements (step 1 and 3, described above). Small frequency components that were not amenable to the Lorentzian curve fit (van Dijk and Wit, 1990) were excluded from further analysis. In our study, the SOAE level is defined by the area under the emission peak. This method allows a precise and robust measure of emission levels, especially if the peak does not fall within one resolution bin. For the subset included in the STC analysis, we further required that the SOAE was suppressed by at least 2 dB by external tones of amplitudes lower than 80 dB SPL. The initial emission recording (step 1) was used to define the SOAE frequencies (f_{SOAE}) and levels. The average frequency of each SOAE in both unsuppressed recordings (step 1 and 3) was used to define the average frequency of the emission ($f_{average}$) used in the suppression analysis.

2.3.1. Stimulus presentation

In order to investigate suppression of SOAEs, brief stimulus tones were presented over a wide range of frequencies and levels. The duration of each tone was 1.2 s, including a 10 m s cosine rise/fall time. SOAE recording started 150 m s prior to the tone onset and ended 150 m s after tone offset. Thus, for each stimulus tone, a segment of 1.5 s of the microphone signal was recorded and stored for later analysis. In one individual, the tone duration was 2.4 s. The stimulus frequencies were chosen to generously cover the range in which SOAEs were detected. In most cases, the suppression frequency varied from 4 to 16 kHz in 1/24 octave steps. In one individual, the step size was 1/16 octave.

The stimulus levels varied between presented frequencies and ears. The widest range was −13 to 81.2 dB SPL in 4 dB steps. In a typical case, with 49 frequencies between 4 and 16 kHz and 22 levels, the total number of stimuli was 1078. The sound pressure levels (SPLs) of the stimuli were roughly equalized according to the frequency response recorded using a Brüel & Kjaer system (type 4136) in a custom-build coupler that mimicked the acoustics of the barn-owl ear canal. Final SPLs were post-hoc corrected using the Etymotic ER10-C readings of actual stimulus levels in the individual ear canal, using a single sensitivity factor for the ER10-C.

2.4. Data analysis

From the microphone recording of a single tone presentation, the effect of that tone on each of the SOAE spectral peaks could be obtained. For each SOAE frequency ($f_{average}$) of interest, the following analysis was carried out.

As described above, for each stimulus tone, a recording of 1.5 s was stored: 0.15 s without stimulus, then 1.2 s with stimulus, followed by 0.15 s without stimulus. The center 1 s of this recording was evaluated. Note that the stimulus tone was on during this entire 1-s interval. The purpose of the subsequent analysis was to determine the amplitude of the SOAE of interest in the presence of the tonal stimulus.

First, a tonal signal with a frequency equal to the stimulus plus two higher harmonics was fitted to the time-domain of the recorded signal. The resulting fit was subtracted from the recorded signal. This provided a residual that included the SOAEs from the barn owl ear, but excluded the stimulus tones and its harmonics. Second, the SOAE frequency of interest was isolated by application of a zero-phase band-pass filter with an amplitude response determined by the average $f_{average}$ and the width of the filter (Δf):

$$A(f) = \left[1 + \frac{\left(2\left[f - f_{average}\right]\right)^{8}}{\Delta f}\right]^{-\frac{1}{2}} \quad (1)$$

The center frequency of the filter was placed at the unsuppressed $f_{average}$ and the width of the filter set to 400 Hz.

The Hilbert phase of the filtered signal was then used to compute the average of the actual SOAE frequency during the 1-s segment. Thirdly, the filter procedure was repeated, but with a filter center frequency that now equaled this computed SOAE frequency, and the filter width was narrowed to 200 Hz. Finally, from the resulting filtered signal, the SOAE level was obtained as the averaged Hilbert envelope.

As described above, the $f_{average}$ was used as the center frequency of the initial filter during the suppression analysis. Whenever the emission frequencies of the initial (step 1) and final recording (step 3) drifted by $\geq$ 200 Hz, this particular SOAE was excluded from the analysis (in total 9.6% of all SOAEs), since the SOAE signal would potentially drift out of the analysis filter and would not be reliably tracked.

By repeating this procedure for each of the stimulus presentations, a full frequency matrix of SOAE amplitudes was obtained. Each matrix element contained the SOAE amplitude for a specific stimulus amplitude and -frequency. This procedure was only able to reliably identify and isolate SOAEs that were more than about ±100 Hz away from a stimulus tone; for stimulus tones closer than this 200 Hz window, we were unable to assess SOAE suppression. For every stimulus frequency, the tone level at which the emission reached 2 dB attenuation was calculated. A 3-point moving average along the level and frequency dimensions was applied to create smoothed matrices. Such a data set was obtained for each $f_{average}$, whenever 2 dB attenuation was reached the smoothed amplitude matrix was computed by linear interpolation between successive tone levels. The results were subsequently combined for various frequencies to calculate STCs. Thus 2 dB STC are characterized by all relevant suppressor-tone frequencies and -levels. The lowest suppression tone level is referred to as the threshold, with a corresponding tip frequency (f_{tip}) of the tuning curve.

According to custom, the Q_{10dB} value, which describes the tuning selectivity was calculated as:

$$Q_{10dB} = \frac{f_{tip}}{\Delta f_{10dB}} \quad (2)$$

Where f_{tip} denotes the STC tip frequency and $\Delta f_{10\,dB}$ the width of the STC at 10 dB above the tip level.

The slopes for the lower and the higher frequency flanks of each STC were evaluated. According to f_{tip}, and to enable direct comparisons with previous work (Taschenberger and Manley, 1997),

two levels 3 dB (L_1) and 23 dB (L_2) above the tuning curve threshold and the corresponding frequencies (f_1 and f_2) were calculated by using an interpolation routine. For each STC, the slopes of the two flanks (below and above f_{tip}) were calculated.

$$S = (L_2 - L_1) / \log_2(f_2 / f_1) \quad (3)$$

Non-parametric analysis of variance was carried out by Kruskal-Wallis and post-hoc Mann-Whitney U testing using SPSS (IBM SPSS Statistics 23, NY, USA).

3. Results

All ears of barn owls ($n = 14$) showed SOAEs, with individual ears having between 9 and 16, on average 12.7 SOAEs. The pattern of SOAEs was unique to each ear. The comparison of right and left ears of each individual revealed no obvious correlation of the SOAE frequencies (f_{SOAE}). The f_{SOAE} ranged from 3.4 to 10.2 kHz. Fig. 1 shows representative individual SOAE spectra. A total number of 178 SOAEs was observed. SOAE levels were clearly above the microphone noise (Fig. 2A). As an example, consider a small peak with a peak level at −20 dB SPL and a spectral width of 200 Hz. The peak level corresponds to 2 μPa. Thus, in the spectrum, the total area under the peak (L) is: $\left(\frac{\pi}{2}\right) \cdot 2^2 \cdot 200 = 1256$ μPa. Hence the peak level (L) equals: $10 \cdot \log_{10}\left(\frac{1256}{20}\right) = 5$dB SPL, which is well above the noise floor for a bandwidth of 1 Hz (Fig. 2A). The noise level is thus substantially lower than the level of small peaks (Fig. 1).

SOAEs overlapped at the base of the amplitudes and thus often formed a plateau that was well above the microphone noise floor and ranged in frequency from approximately 6.5 kHz−10 kHz. Fig. 2B shows that the emission peak width, determined from the Lorentzian curve fit, did not strongly correlate with SOAE level ($R^2 = 0.0034$). SOAEs were nearly regularly spaced on a linear frequency axis (Fig. 2C), with a median distance of 430 Hz (interquartile range of 179 Hz, range from 363 Hz to 542 Hz).

SOAE were stable within 1 dB over the time needed to obtain the recordings. Comparing f_{SOAE} before and after presentation of external tones (steps 1 and 3, see Methods) showed maximal differences of around 300 Hz, and more typically less than 100 Hz.

3.1. Characteristics of suppression tuning curves

For 73 SOAEs, at least 2 dB of suppression was observed; most of these had a high f_{SOAE} and thus fell within the auditory fovea (>5 kHz). STCs were V-shaped and selectively tuned (Fig. 3A). The majority of the 73 SOAEs with STCs (71.2%) originated from the upper half of the auditory fovea, between 7.5 and 10 kHz. The tip of the STC could fall on either side of the emission frequency. In 76.7% of cases, the STC tip was above the emission frequency.

The slope for each STC flank was measured between 3 and 23 dB SPL above the STC tip. For 18 STCs, this suppression range was available on both flanks. The STC slope of the high-frequency flank (median: 179.9 dB/octave) was steeper than that of the low-frequency flank (median: −76.5 dB/octave). At higher levels, both the low- and high-frequency flank flattened out (Fig. 3A).

3.1.1. Tuning curve threshold

The thresholds of the 2 dB STCs varied from 7.0 to 57.5 dB SPL, with no trend across $f_{average}$ ($R^2 = 0.05$; $p = 0.07$). Fig. 3B shows that narrower SOAEs were suppressed by external tones of lower sound pressure levels than spectrally broader SOAEs ($R^2 = 0.39$; $p < 0.001$). Furthermore, SOAEs with relatively lower levels required a higher sound level for suppression, whereas larger SOAE levels were suppressed by tones of lower sound pressure levels (Fig. 3C; $R^2 = 0.36$, $p < 0.001$). A comparison of the methods to derive SOAE levels of Taschenberger and Manley (1997; peak level) and our study (area under the peak) was carried out on our new data, to assess the difference that it potentially makes to the results. Peak levels were typically 10 dB lower. In order to show SOAE levels of both studies in a comparable way, we therefore added 10 dB to all the Taschenberger and Manely (1997) data (Fig. 3C).

In order to compare the STCs to neural tuning curves (TCs) in the same species, data from two previous reports were plotted together with the results of the present study (Fig. 4A). Taschenberger and Manley reported a median STC threshold of 11 dB SPL ($n = 8$), and the median neural TC threshold was 14 dB SPL ($n = 246$; Köppl, all

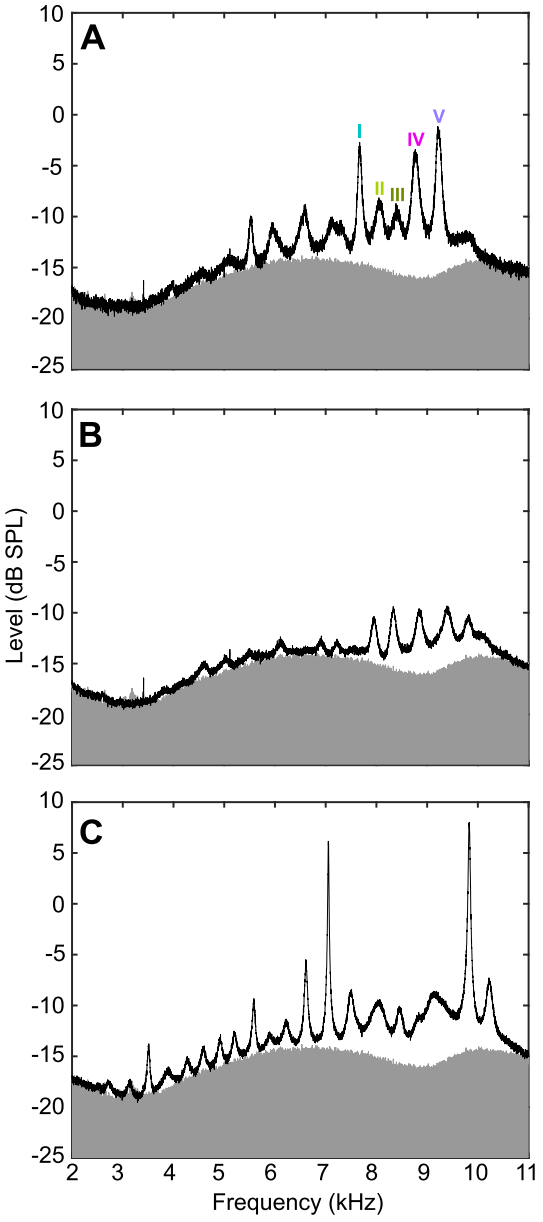

Fig. 1. Three spectra of unsuppressed spontaneous otoacoustic emissions (SOAEs) of the barn owl. The spectral peaks correspond to the faint emission tones produced spontaneously from individual ears. Each ear showed a specific pattern of peak frequencies and amplitudes. In panel (A) 5 peaks are labeled: (I) at 7.67 kHz, (II) at 8.05 kHz, (III) at 8.40 kHz, (IV) at 8.77 kHz, and (V) at 9.23 kHz. The filled background shows the noise floor of the recording system. The spectral resolution is in 1-Hz bands.

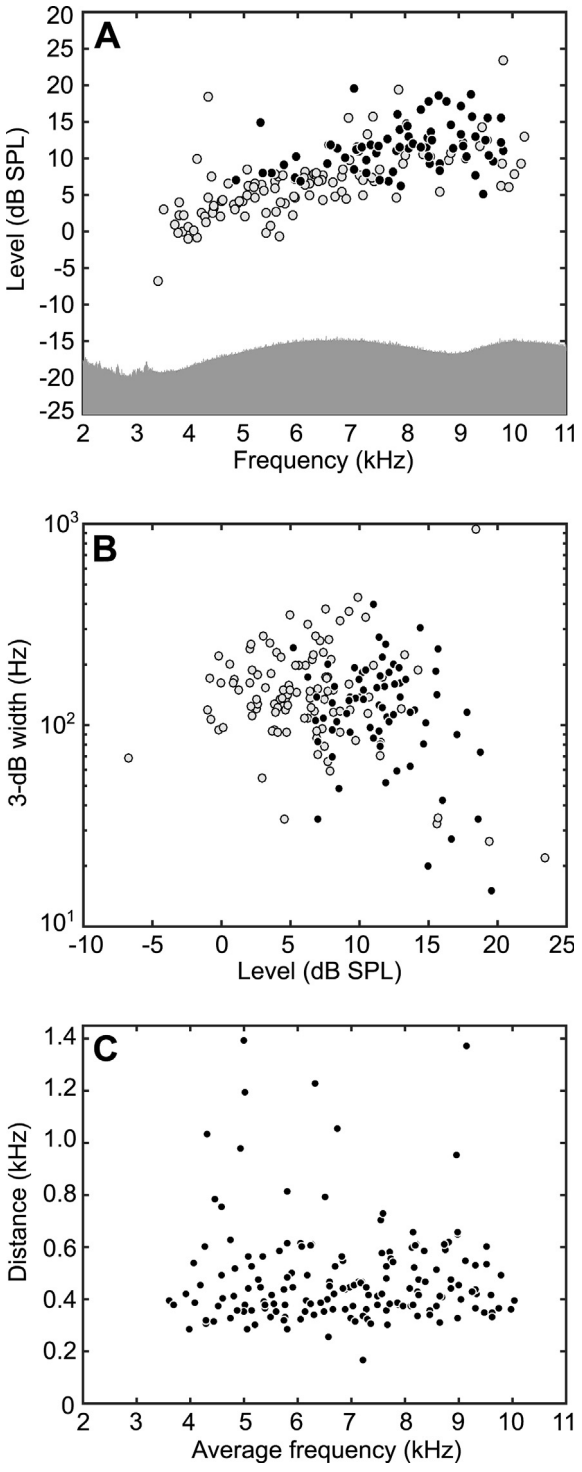

Fig. 2. Characteristics of spontaneous otoacoustic emissions (SOAEs). Each circle corresponds to one SOAE peak (n = 178). For the SOAEs represented by black-filled circles in panels (A) and (B), suppression tuning curves were obtained (STCs, n = 73). (A) Relationship between SOAE frequency and SOAE level. The filled background shows the noise floor of the recording system in 1-Hz bands. (B) SOAE peak width in relation to SOAE level. (C) Frequency distance between neighboring unsuppressed SOAE peaks (median distance = 430 Hz). The average frequency of each SOAE ($f_{average}$) was defined by the averaged spectrum of both unsuppressed recordings (see Methods, step 1 and 3).

data shown in Fig. 4A). In the present study, a higher median STC threshold was obtained (30.80 dB SPL, n = 73). A Mann-Whitney U test revealed significant differences ($p < 0.005$) between the STC thresholds of this study compared to suppression thresholds reported in 1997 by Taschenberger and Manley (U = 60) and this current study compared to neural TC thresholds reported by Köppl (1997a), b, and unpublished results (U = 2633.5).

3.1.2. Tuning curve Q_{10dB}

The STC median Q_{10dB} value was 4.87 (n = 73). Q_{10dB} was independent both of SOAE level ($R^2 = 0.0012$; $p = 0.77$) and of SOAE width ($R^2 = 0.012$; $p = 0.36$). Q_{10dB} values of this study were compared to previous suppression- and neural TCs (Fig. 4B). Taschenberger and Manley reported a median Q_{10dB} of 8.2 (n = 8) and the neural TC dataset of Köppl (1997a, b and unpublished results) revealed a median Q_{10dB} of 5.7 (n = 218). The Mann-Whitney U test showed significant differences between the Q_{10dB} values of the current STC study and the STCs study published 1997 by Taschenberger and Manley ($U = 23$, $p < 0.05$) and between the current study and the neural TCs published by Köppl (1997a, b), and unpublished results ($U = 10935$, $p < 0.05$).

4. Discussion

4.1. General characteristics of the SOAEs

As in mammals, SOAEs are rare in birds. The barn owl is thus far the only known bird species showing SOAEs. Considering that SOAEs have been reported in all groups of land vertebrates, it is assumed that these emissions are caused by a symplesiomorphic active process that evolved in ancestral species and constitutes a fundamental feature of all inner ears (Manley, 2001). In mammals, but not in birds, it is further assumed that emission energy originates by the action of prestin (Dallos et al., 2008; Xia et al., 2016). The emission patterns are specific for each species and individual (Manley, 2001), suggesting that the species' and individual's morphology affects spectral patterning. In birds, the degree of interaural coupling in general decreases with both increasing head size and increasing frequency. For the barn owl, it has been shown that interaural attenuation increases to values of minimally 35 dB at 7 kHz and above (Moiseff and Konishi, 1981; Palanca-Castán et al., 2016). Thus, most or all of the measured SOAEs are not expected to interact between the ears and we also found no evidence for such interactions. Many studies have shown that the widespread phenomenon of SOAE suppression relates to individual frequency tuning properties (Manley and van Dijk, 2008).

In this study, many more SOAEs per ear, in particular ones with smaller levels, were recorded than 20 years ago by Taschenberger and Manley (1997; comparison in Fig. 3C). This is presumably due to the higher sensitivity of the equipment used.

If SOAE in any individual ear did shift in frequency, all SOAE shifted in the same direction, suggesting a common influence such as minor variations in body temperature (that have large effects, see Taschenberger and Manley, 1997) or possibly changes in tonic efferent activity (Manley et al., 1999).

The distance between neighboring SOAEs was near 430 Hz in all frequency ranges and across ears (Fig. 2C and Supplementary Fig. 1). This contrasts with emission spectra in humans, where the spacing between SOAE peaks increases with increasing frequency of the neighboring peaks (reviewed in Shera, 2003). The spacing in human SOAE spectra presumably reflects standing-wave conditions for which backward and forward traveling waves in the cochlea can combine to produce a standing wave on the basilar membrane. In lizard SOAE spectra also, the spacing generally increases with the peak frequency (Manley et al., 2015). In birds, including barn owls, sharply tuned traveling- or standing waves presumably do not exist on the basilar membrane, since in pigeons and chickens only broadly-tuned traveling waves without evidence

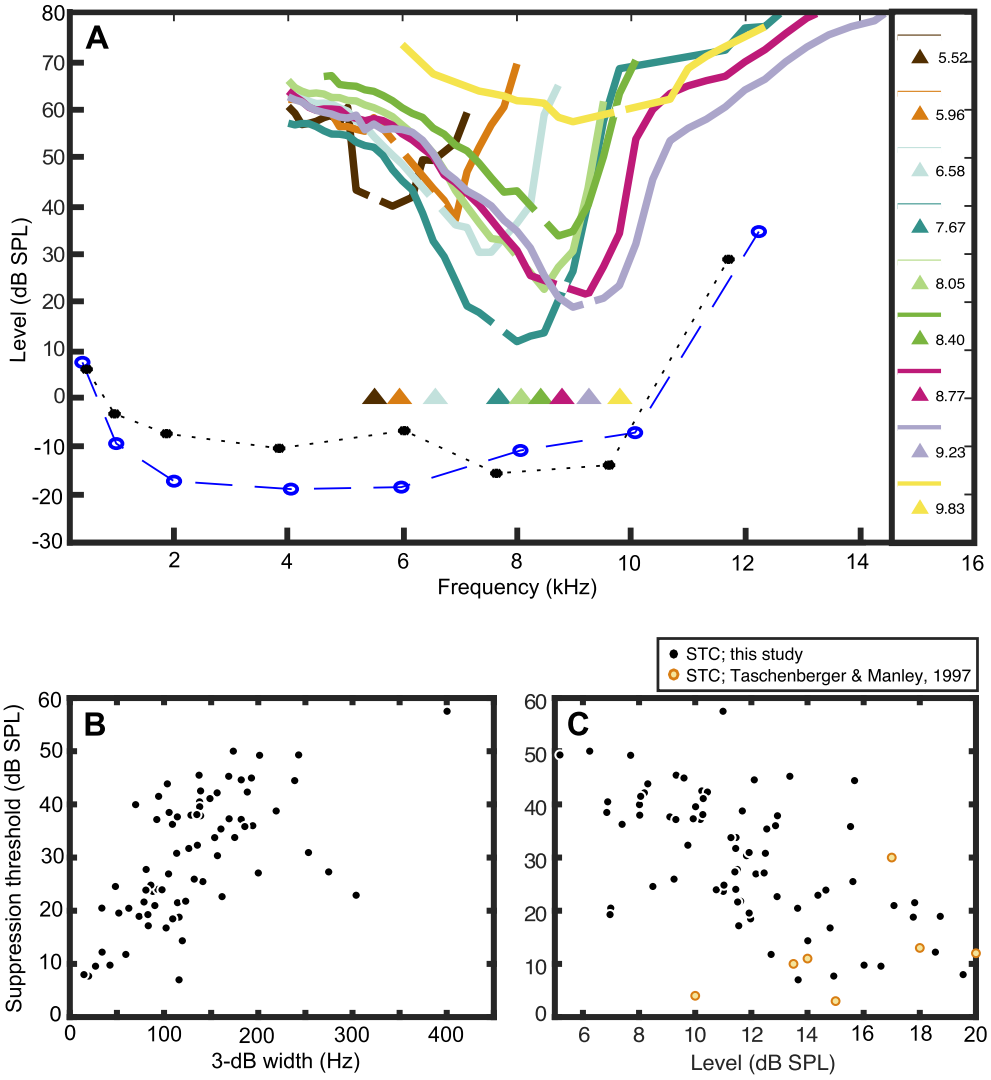

Fig. 3. Suppression of spontaneous otoacoustic emissions (SOAEs). Suppression tuning curves (STCs) indicate the stimulus level needed for 2 dB suppression of the SOAE. (A) The STCs of one individual (spectrum in Fig. 1A). The triangles indicate the SOAE frequencies. The colors match the corresponding STC. The stimulus frequencies within 200 Hz of the unsuppressed spontaneous emission frequency were omitted (see main text) and appear as gaps in the STC. Behavioural thresholds in the barn owl are shown for reference, as black dotted lines (Krumm et al., 2017) and blue dashed lines (Konishi, 1973). (B) STC threshold as a function of unsuppressed SOAE width. (C) STC threshold as a function of unsuppressed emission level. Black-filled circles indicate STCs from this study (n = 73) and filled orange circles data from Taschenberger and Manley (1997; n=7). Note that 10 dB were added to the SOAE levels from Taschenberger and Manley (1997), to correct for the different methods in level estimation between both studies. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

for nonlinear amplification were observed (Gummer et al., 1987; Xia et al., 2016). This is in apparent contrast with independent evidence for cochlear amplification and nonlinear behavior, such as the high sensitivity and sharp tuning of auditory nerve fibers, otoacoustic emissions, and active motile processes in hair cells (e.g., Manley, 2001; Peng and Ricci, 2011; Beurg et al., 2013). Although membrane channel densities and kinetics (electrical tuning) contribute to sharp frequency tuning, this component fades towards the upper frequency range of bird hearing, above several kHz (Wu et al., 1995), i.e. in the frequency range of particular interest in the barn owl.

4.2. SOAE suppression by external tones

In all classes of terrestrial vertebrates so far studied, SOAEs have been shown to be sensitive to the presence of external tones, especially near their peak frequency. In barn owls, also, SOAE level was suppressed by external tones, depending on the frequency distance between the external stimuli and the SOAE and on stimulus level. Stimuli closer in frequency to the SOAE had a larger suppressive effect than those further away, and tones of higher level were more suppressive than those of low level. Thus the typical V-shaped STCs were observed. The suppression tuning curves obtained here were similar in their shape to those observed in the earlier study of barn owls (Taschenberger and Manley, 1997).

4.2.1. Tuning curve tip and frequency pushing and pulling

In humans, the tip frequency of STC is consistently found above the SOAE frequency (Schloth and Zwicker, 1983; Zizz and Glattke, 1988; Manley and van Dijk, 2016: 4.5% higher). In our study, the most effective suppressor stimulus in owls was either below or above the SOAE peak frequency, with a tendency that STC tips lay above emission frequency. Due to the analysis procedure, it was not possible to fully evaluate the tip region of the STCs, i.e. stimulus frequencies within ±100 Hz of the emission frequency.

Geisler et al. (1990) described a mammalian cochlear model that

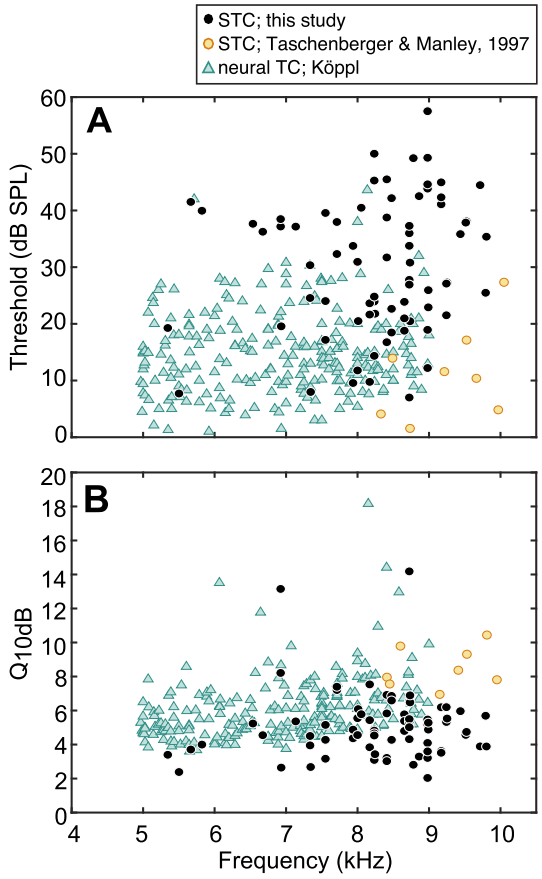

Fig. 4. Comparison between tuning curves of SOAE suppression and auditory-nerve single-unit recordings. (A) Thresholds of STCs and neural TCs as a function of tuning curve tip frequency. (B) The filter quality factor Q_{10dB} of STCs and neural TCs as a function of tuning curve tip frequency. SOAE suppression tuning curves: filled black circles (this work) and filled orange circles (Taschenberger and Manley, 1997). Neural tuning curves: filled turquoise green triangles (Köppl, 1997a, b, and unpublished results), for the frequency range from 5 to 10 kHz. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

examined the source of SOAEs and the shift in STC tip frequency towards higher frequencies. This model might not be applicable to all vertebrates with SOAEs (e.g. lizards and barn owls), as it requires mammal-like traveling waves and a mammalian active mechanism; consequently other models have to be considered (e.g. Bergevin and Shera, 2010). Earlier SOAE suppression studies in other species, such as lizards (Köppl and Manley, 1994; Manley et al., 1996; Manley, 2004, 2006), described f_{SOAE} changes caused by external tones. Generally, the f_{SOAE} shifted away from the stimulus frequency (frequency "pushing"), especially when the stimulus frequency was above the emission frequency. Stimuli of greater sound pressure level and frequency nearer the emission frequency increased the f_{SOAE} shift up to several hundred Hz (Köppl and Manley, 1994; Manley et al., 1996; Manley, 2004). Human SOAEs can also be both pushed away from or pulled towards an external stimulus (Long, 1998; Baiduc et al., 2013; Manley and van Dijk, 2016). This SOAE shift is, however, very much smaller in humans than in lizards. Presumably, human SOAEs are frequency stabilized by the standing-wave mechanisms discussed above.

Interestingly, in barn owls we did not observe consistent pushing or pulling of the SOAEs that depended on stimulus level or frequency (Supplementary Fig. 2). It is currently not clear why barn owl SOAEs are relatively stable in frequency when being suppressed by external tones, despite the presumed absence of standing waves that may serve as a stabilizing mechanism.

4.2.2. Tuning curve slopes and secondary side lobes

The asymmetric shape of STCs, with steeper slopes for the high-frequency flank (human: e.g. Zizz and Glattke, 1988, Manley and van Dijk, 2016; macaque monkey: Martin et al., 1988; most lizards: Manley and van Dijk, 2008) or the lower frequency flank (some lizards: Manley, 2006) describes an almost universal phenomenon of asymmetrical inner-ear tuning. Comparable tuning curves for neural tuning (lizards: Manley et al., 1990; Köppl, 1997a; Manley, 2001) and STCs within the same species (e.g. Martin et al., 1988; Manley and van Dijk, 2016) have been reported. Consistent with neural tuning curves of the barn owl (Köppl, 1997a), SOAE-STCs were characterized by a steeper slope of the higher-frequency flank.

Unlike other species, such as humans (Manley and van Dijk, 2016), macaque monkey (Martin et al., 1988), and many lizards (Köppl and Manley, 1994; Manley, 2001), the STCs of barn owls lacked very sharp secondary sensitivity tips on the high-frequency flank of STCs (Taschenberger and Manley, 1997) and of neural TCs (e.g. Köppl, 1997a). Consistent with Taschenberger and Manley (1997) we found, however, that the high-frequency flank of some STCs flattened out towards the high suppressor levels, something which was never observed in neural TCs. In humans, the side lobes were attributed to the interactions between the suppressing stimulus and the SOAE standing wave (Manley and van Dijk, 2016).

The absence of secondary suppression lobes in the barn owl can be interpreted as standing waves not being present. This may reflect expected differences in the cochlear mechanics of the barn owl compared to mammals. Note that these secondary minima were also seen in neural tuning curves in the bobtail and other lizard species (e.g, Manley, et al., 1988). However, the side lobes of STCs and neural tuning curves in lizards cannot be caused by standing waves, as suggested for humans, as there are no traveling waves on the basilar membrane (e.g., Manley, et al., 1988). The inconsistent presence of side lobes in suppression tuning curves and neural tuning curves suggests different inner ear tuning mechanisms in mammals, birds and lizards.

Behaviourally obtained hearing thresholds of the barn owl indicated sensitive hearing between 200 Hz and 12 kHz (Konishi, 1973; Krumm et al., 2017). However, SOAEs were also suppressed by higher-level (>~55 dB SPL), high-frequency external sounds above the behaviourally tested hearing range. High-frequency STC flanks reached up to the very highest frequency of the owl's hearing range and even extended it (Fig. 3A). Consequently, we suggest that behavioural hearing threshold estimation should include frequencies above 12 kHz.

4.2.3. Tuning curve tip thresholds and their relation to SOAE width and level

An unexpected observation was that both SOAE level and width were related to STC tip threshold, such that narrower and larger SOAE suppressed more easily, with lower thresholds (Fig. 3B and C). At present, we can only speculate on the origin of these correlation by considering simple oscillator models (Stratonovich, 1967). The models tend to suggest a relation between oscillator amplitude and suppression threshold that is reverse to what has been observed here: in the oscillator model the effectiveness of an external force (amplitude E) to modulate a self-sustained oscillation (amplitude A) always depends on the ratio E/A. The larger the oscillator amplitude A, the stronger the external force E is needed to affect the oscillator's behavior. In the current work, the reverse appears to be true. The relation between suppression threshold and the ratio E/A of an external suppressor tone (E) and the oscillation amplitude (A), assumes that the internal noise level, to which the oscillator is

exposed, is relatively constant. Specifically, the noise level is considered to be constant across SOAEs with various oscillation amplitudes. This assumption appears to be approximately correct for human SOAEs, where a negative correlation between SOAE width and level was found (Talmadge et al., 1993; van Dijk et al., 2011). However, in the barn owl, SOAE peak height and width are not significantly correlated (Fig. 2B). As a consequence, the internal noise of the SOAE oscillator is not at a constant level across SOAE peaks. The oscillators internal noise counteracts its synchronization to an external tone. Thus, less internal noise implies easier synchronization with lower suppression thresholds. Consistent with this view, relatively narrow SOAEs have low suppression thresholds (Fig. 3B).

The STC results of the present study were plotted together with the already published STCs and neural TCs of the barn owl (Fig. 4A). Between 5 and 10 kHz, both STC measurements (Taschenberger and Manley, 1997) and TCs of single auditory nerve fibers (Köppl, 1997a, b, and unpublished results) show similar best thresholds. In the present study, a higher STC threshold was obtained which, however, falls within the range of the previously observed thresholds (STC: 1.55–27.33 dB SPL, neural recordings: 1–43.6 dB SPL). This is plausibly explained by the negative correlation between SOAE suppression threshold and SOAE level: weak SOAEs have high suppression thresholds (Fig. 3C) and the more sensitive recording equipment allowed the recording of many more small SOAEs. Consequently, overall SOAE suppression thresholds are higher in the current study when compared to Taschenberger and Manley (1997).

4.2.4. STC sharpness: Q_{10dB}

Here, the current data are compared to previous reports of STCs (Taschenberger and Manley, 1997) and neuronal TCs Köppl (1997a, b and unpublished results) of the barn owl (Fig. 4B), within the overlapping frequency range from 5 to 10 kHz. The Q_{10dB} values were similar, but lower in the current study.

Another difference to previous findings was the absence of any frequency dependence on tuning sharpness in our data. Köppl (1997a) showed that barn-owl eighth-nerve axons were narrowly tuned, even at SPLs much above CF threshold. The mean neural Q_{10dB} increased with CF according to a power law from 1.7 at 0.5 kHz to 7.25 at 9 kHz (Köppl, 1997a). Similarly, in behavioural data, the auditory filter bandwidth increases within the auditory fovea (Dyson et al., 1998). In contrast, the SOAE suppression measurements described here did not reveal such a trend; a regression across SOAE-STC sharpness data was flat (Fig. 4B).

In humans and in lizards, there is a clear trend for STC tuning sharpness to increase with frequency (Manley et al., 2015). If this reflects the logarithmic distribution of frequencies in the tonotopy of the papillae of these species, then the lack of such an increase in the barn-owl data simply reflects the almost linear distribution of approximately 80% of the frequency range of its cochlea (Köppl et al., 1993).

In summary, STCs are similar to neural TCs in some details but were, on average, less sensitive and less sharply frequency tuned (Fig. 4B), especially at high sound levels. For several species, Q_{10dB} values of SOAE-STCs were found to be equivalent to neural tuning curves derived from auditory nerve fiber recordings (e.g.: compare barn owl: Taschenberger and Manley, 1997 with Köppl, 1997a; macaque: Martin et al., 1988 with Shera et al., 2011, lizards: Manley et al., 1990 with Köppl and Manley, 1994). However, the current study does not confirm this impression of detailed similarity between neural and suppression TCs, despite apparent support from the smaller sample in the work of Taschenberger and Manley (1997). This cannot be explained by sampling biases for different types of TCs. In birds, including the barn owl, there is no evidence for populations of auditory nerve fibers with distinct physiological properties. In particular, there are no subgroups distinguished by spontaneous discharge rate, since spontaneous rates show a monomodal distribution. There is also no correlation between spontaneous rate and other physiological properties such as response threshold or tuning sharpness (e.g., Köppl, 1997a, 2011).

In mammals under ideal recording conditions (Sellick et al., 1982; Rhode, 1995; Narayan et al., 1998), tuning at the basilar membrane level matches recordings of single auditory nerve fibers. This is unlikely to be the case in birds. Although equivalent measurements are not available for barn owls, in both chicken and pigeon, basilar-membrane motion showed poorer frequency tuning than auditory-nerve fibers, and no clear evidence for active amplification (Gummer et al., 1987; Xia et al., 2016).

5. Conclusions

In this study, SOAEs of both ears in 7 barn owls were recorded and suppressed by pure-tone stimulation. The frequency separation between neighboring peaks was approximately constant across frequency. Unlike in humans and lizards, secondary dips of suppression on the high-frequency flanks of STCs were not found. This suggests that peripheral processing of SOAE suppression in birds - or at least in the barn owl - differs in this respect from that of lizards and humans. The negative correlation between SOAE width and sensitivity to suppression and the constant frequency spacing to SOAE peaks are likely to be indicators of fundamental properties of the owl's inner ear.

Declaration of competing InterestCOI

The authors declare no competing financial interests.

Contributors

S.E., P.v.D., G.A.M., and C.K. designed the study and performed the measurements. S.E., P.v.D., G.A.M., C.K., and E.d.K., performed the analysis and wrote the manuscript. All authors verified and approved the final manuscript.

Acknowledgements

We thank Paolo Toffanin for programming. This work was supported by the European Union's Horizon 2020 research and innovation programme under the Marie Sklodowska-Curie grant (EGRET cofund, No. 661883) and the DFG Cluster of Excellence EXC 1077/1 "Hearing4all".

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.heares.2019.107835.

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